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## TAXONOMY OF HAPLOPAPPUS, SECTION ISOPAPPUS (COMPOSITAE) ${ }^{1,2}$

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Haplopappus divaricatus (Nutt.) Gray is a wide-ranging, herbaceous annual which is found in sandy soil throughout most of the Coastal Plain of the southern and southeastern United States. Because of differing chromosome numbers reported for H. divaricatus ( $n=4$, Turner \& Ellison, 1960, as Croptilon divaricatum Raf.; $n=5$, Jackson, 1959), a study of the taxon was undertaken in 1961. An aneuploid chromosome series was discovered in which the different chromosome numbers were found in morphologically recognizable entities (Smith, 1964). These are designated Haplopappus divaricatus $(n=4), H$. rigidifolius $(n=5), H$. validus subsp. validus $(n=5)$, H. validus subsp. torreyi ( $n$ $=6$ ), and $H$. validus subsp. graniticus $(n=7)$. Formal taxonomic recognition of the new taxon and new combinations is given in a later section. A metaphase I configuration of $H$. rigidifolius is shown in Fig. 1. Configurations of the other taxa at $\mathrm{M}_{1}$ have been presented earlier (Smith, 1964).

Haplopappus divaricatus and relatives have been recog-

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Figure 1. Meiotic metaphase I of Haplopappus rigidifolius. The vertical reference line $=$ about 4 microns. Inked-in tracing from a photograph.
nized in several different genera, including Inula, Chrysopsis, Croptilon, Diplopappus, Isopappus, and Aster, as indicated in the synoymy given later. Recently, however, this group has been treated as either section Isopappus of Haplopappus (Hall, 1928) or as the separate genus Croptilon (Shinners, 1951). Hall's treatment included H. divaricatus (Nutt.) Gray and H. occidentalis Hall. The latter has since been recognized as Benitoa occidentalis (Hall) Keck (Keck, 1956). Blake (1932) referred a new species from Mexico, Haplopappus bartlettii (as "Aplopappus"), to section Isopappus but this entity was later transferred to Heterotheca by Johnston (1957). I have examined the holotype of $H$. bartlettii (Bartlett 10046, MICH), plus a second specimen (Muller 2854, MICH), and found that the entity differs in numerous details from other section Isopappus taxa. Its general appearance is characteristic Heterotheca and I would concur with Johnston's placement of it there, at least until considerably more information (biosystematic, cytogenetic) on it becomes available.

Shinners' treatment included the single species Croptilon divaricatum (Nutt.) Raf., with varieties divaricatum, hirtellum (Shinners) Shinners, and hookerianum (T. \& G.) Shinners.

Although my own work has been at the specific and infraspecific level, I see no reason to treat the section as a separate genus and, for the present at least, I prefer to follow Hall (1928) in this regard.

## METHODS AND MATERIALS

Field studies were made throughout the range of Haplopappus divaricatus, including Kansas, Oklahoma, Arkansas, Texas, Lousiana, Mississippi, Alabama, Florida, Georgia, South Carolina, and North Carolina. Live transplants and seeds were collected for hybridization studies, buds were fixed in a modified Carnoy's solution ( $95 \%$ ethanol, chloroform, propionic acid; 2:1:1) for cytological analysis, and herbarium specimens were taken for later examination and measurement. Meiotic chromosome counts were made from anther squashes in propio-carmine. Mitotic counts were made from root tip squashes in aceto-orceine, following a $3-5$ minute hydrolysis in $15 \% \mathrm{HCl}$.

Hybridizations between pairs of the taxa were attempted in all combinations. The technique used in the crosses was the same as described by Jackson (1962), except the crossing of two particular heads was made only once and many different heads were used. All taxa in the section are selfincompatible.

The $\mathrm{F}_{1}, \mathrm{~F}_{2}$, and backcross progeny were grown in the greenhouse. Pollen stainability of each plant was sampled by staining $20-30$ minutes in Aniline Blue ( $0.1 \%$ ) in lactophenol and counting a minimum of 300 grains per sample. Those grains staining deep blue were counted as stainable; grains not evenly stained were counted as non-stainable. Later, an apparently equally accurate and much more rapid stain was used: Aniline Blue (water soluble, c. $0.2 \%$ ) in $90 \%$ propionic acid (propionic acid: water, $9: 1$ ). With this stain, counting can begin within 60 seconds after preparation of the slide.

## RESULTS

Table 1 contains a synopsis of the major quantitative characters by which the taxa differ. Formal and more complete descriptions of the taxa are given in a later section. Table 2 shows chromosome counts from field collections of the different taxa made during 1962-64. Voucher specimens for at least one count of each taxon are in the University of Kansas Herbarium. Generally 1-2 (-14) counts were


Figure 2. Known distribution by county of the taxa in section Isopappus. Circles $=$ Haplopappus divaricatus $(n=4)$; squares $=H$. rigidifolius $(n=5) ;$ parabolas $=H$. validus subsp. validus $(n=5)$; triangles $=H$. validus subsp. torreyi $(\mathrm{n}=6) ;$ rectagles $=H$. validus subsp. graniticus ( $n=7$ ).
made per population. Additional counts from first and second generation plants grown in the greenhouse from random seed collections of wild populations would make the total number of counts about double the number shown in Table 2.

The count under subsp. graniticus marked with an asterisk is the only evidence of euploidy found in the field in the section. A single plant of this makeup was found in 1962 and previously reported as "morphologically $n=7$ with anomalous pairing" (Smith, 1964). Reexamination of permanent slides of meiotic material from the plant show it is a simple triploid.

Supernumerary chrosomes occur in a low frequency in subspecies of Haplopappus validus. Their absence in $H$. rigidifolius (Table 2) may be due to insufficient sampling,
while in $H$. divaricatus they appear to be absent or rare. The supernumerary chromosomes are small and near-metacentric, presumably consisting only of a centromere and adjacent chromatin.

Figure 2 is a distribution map by county of the five taxa. Most of these locations were visited by the author. However, numerous locations were obtained from specimens from various herbaria, particularly the excellent collection of the University of North Carolina.

Table 1. Synopsis of key quantitative characters of taxa in the section Isopappus. The first number is the range, the second (underlined) is the arithmetic mean, the third is the standard deviation. Based on measurements from 25-40 individuals of each taxon. divar. $=H$. divaricatus; rigid. $=H$. rigidifolius; validus $=H$. validus subsp. validus; torreyi $=H$. validus subsp. torreyi; granit. $=H$. validus subsp. graniticus.

| Character | divar. | rigid. | validus | torreyi | granit. |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Hgt. to 1st <br> head (cm) | $30-97$ | $6-97$ | $20-81$ | $19-88$ | $16-51.5$ |
|  | 59.7 | 51.8 | 49.7 | 46.7 | 31.8 |
|  | 18.8 | 22.8 | 14.3 | 13.3 | 8.8 |
| Number of | $5-11$ | $5-22$ | $13-29$ | $10-17$ | $10-21$ |
| ray flowers | 8.1 | 14.6 | 19.7 | 14.4 | 16.6 |
|  | 1.4 | 4.8 | 1.0 | 1.8 | 3.2 |
| Number of | $9-26$ | $6-60$ | $33-108$ | $23-51$ | $20-79$ |
| disc | 15.8 | 28.2 | 59.2 | 38.2 | 45.9 |
| flowers | 3.9 | 15.7 | 15.9 | 7.2 | 16.9 |
| Ligule | $3.9-6.0$ | $4.0-7.4$ | $6.0-12.0$ | $5.7-11.0$ | $6.3-14.0$ |
| length (mm) | 5.29 | 5.31 | 9.16 | 8.30 | 9.96 |
|  | 0.59 | 0.90 | 1.42 | 1.28 | 2.04 |
| Ligule | $1.9-3.2$ | $1.7-2.6$ | $1.8-3.1$ | $2.4-3.3$ | $2.7-5.0$ |
| width (mm) | 2.39 | 2.28 | 2.48 | 2.87 | 3.86 |
|  | 0.34 | 0.28 | 0.31 | 0.25 | 0.58 |
| Involucre | $5.0-7.0$ | $4.5-8.0$ | $5.5-8.0$ | $5.0-9.5$ | $5.5-10.0$ |
| height (mm) | 608 | 6.04 | 7.01 | 7.23 | 7.76 |
|  | 0.53 | 0.99 | 0.59 | 0.84 | 1.28 |
| Receptacle | $25-4.0$ | $1.8-5.0$ | $4.0-7.0$ | $3.5-6.0$ | $3.9-6.0$ |
| diameter (mm) | 3.01 | 3.54 | 5.35 | 4.83 | 4.89 |
|  | 0.39 | 0.95 | 0.72 | 0.40 | 0.69 |
|  |  |  |  |  |  |

Table 2. Chromosome counts made from field collections of the different taxa during 1962-64. Designations for the taxa follow the scheme of Table $1 . \mathrm{su}=$ supernumerary univalent; $\mathrm{sp}=$ supernumerary pair; III = trivalent, $\mathrm{II}=$ bivalent, $\mathrm{I}=$ univalent.

|  | $\begin{array}{l}\text { No. locations No. plants } \\ \text { sampled }\end{array}$ |  | Chromosome number |
| :--- | :---: | :---: | :--- |
| counted |  |  |  |$]$.

The results of attempted hybridization between pairs of the taxa are shown in Figure 3. $\mathrm{F}_{1}$ hybrids were generally vigorous and intermediate in most characters. They flowered somewhat later than the average time of the parental taxa. Minor aberrations, such as chlorotic spotting and striping, fused leaves, and abortion of the first few heads occurred at a low frequency in the $\mathrm{F}_{1}$ hybrids. One voucher specimen of each successful $\mathrm{F}_{1}$ hybrid conbination (Fig. 3) is in the University of Kansas Herbarium.

Only a few $\mathrm{F}_{2}$ plants were produced from most of the different $\mathrm{F}_{1}$ 's, despite numerous crosses. Table 3 gives the results of pollen stainability tests of the $\mathrm{F}_{2}$. Essentially all crosses involving Haplapappus rigidifolius failed completely

Table 3. Pollen stainability of $\mathrm{F}_{2}$ progeny. Designations for taxa follow the scheme of Table 1.

| $\mathrm{F}_{2}$ | No. plants | Pollen |  |
| :--- | :---: | :---: | :---: |
|  |  | Rtainability $(\%)$ |  |
| Range | Average |  |  |
| divar. $\times$ validus | 20 | $11.9-99.3$ | 69.3 |
| divar. $\times$ torreyi | 15 | $5.3-92.2$ | 33.6 |
| divar. $\times$ granit. | 1 | - | 95.6 |
| validus $\times$ granit. | 6 | $39.3-70.3$ | 54.6 |
| torreyi $\times$ validus | 3 | $42.4-63.7$ | 53.0 |
| torreyi $\times$ granit. | 29 | $32.7-99.7$ | 76.4 |



Figure 3. Crossing polygon, showing avenues for gene exchange among taxa in the section Isopappus, based on average pollen stainability of $\mathrm{F}_{1}$ hybrids. The width of the avenues connecting the taxa is proportional to the average pollen stainability of the $F_{1}$ hybrids. Average pollen stainability is given, with the number of individuals tested following in parentheses. Arrows on the avenues point toward the pistillate parent in crosses in which successful $\mathrm{F}_{1}$ 's were obtained in one direction only. $\mathrm{F}_{1}$ seed was obtained in the cross subsp. validus (pistillate) $\times$ subsp. torreyi (staminate), but all resultant progeny died in the seedling stage. The dotted line indicates that the attempted hybridization failed in both directions.
in the $\mathrm{F}_{2}$. One cross, $H$. validus subsp. torreyi $\times H$. rigidifolius, is represented in the $\mathrm{F}_{2}$ by a mere two seedlings presently growing in the greenhouse.

A small number of backcross progeny were obtained. However, since the number of these was low and their aver-
age pollen stainability did not differ significantly from that of the $\mathrm{F}_{2}$, they are not included in Table 3.

Benitoa occidentalis would not hybridize with either $H$. validus subsp. validus or subsp. graniticus. This evidence while negative, lends genetic support to Keck's (1956) recognition on morphological grounds of $H$. occidentalis as the monotypic genus Benitoa.

## DISCUSSION

The synopsis of quantitative characters separating the taxa in section Isopappus (Table 1) shows that there is considerable overlap for these characters. It is pertinent here to point out that, for the most part, plants from which the measurements were taken were selected to show the range of morphological variation found in the field and that the characters listed in Table 1 are influenced more or less strongly by environmental conditions. Available moisture influences the number of disc and ray flowers and thus head size, the width of the leaves, the amount of serration of the leaves, and the height of the plant. Thus, under drought conditions, the plants tend to be shorter, with fewer ray and disc flowers (hence, smaller heads), and narrower leaves which tend toward entire margins or serrulation apically. A similar effect is seen in late season forms with regard to head size. Collections of $H$. validus subsp. validus made after about mid-September and of $H$. rigidifolius after about mid-November tend to have much smaller heads (with reduced numbers of disc and ray flowers). Nevertheless, if collections are made during normal peak blooming period from populations under more or less normal environmental conditions, the overlap is relatively small. The quantitative characters (Table 1) combined with the qualitative characters of peduncular pubescence are generally sufficient to distinguish the taxa with ease.

Haplopappus rigidifolius is sharply delimited from the other taxa in the section by its lack of glandular stipitate pubescence on the peduncles. $H$. divaricatus is likewise easily distinguished in the vast majority of cases from $H$.
validus by its small heads. It is only in $H$. validus that the overlap becomes a problem, and that is precisely one of the reasons for placement of the entities validus, torreyi, and graniticus at the subspecific level. These three entities overlap in morphology but have different means, are separated at least partially by sterility barriers, and are mostly allopatric in their distributions (Fig. 2). Where they overlap geographically, or closely aproach one another, there is evidence of a low frequency of hybridization (at least between validus and torreyi).

The distributions of the taxa overlap somewhat in southern Texas (Fig. 2). This sympatry, however, is more apparent than real. All of the taxa generally occur in small, localized populations, covering several square acres to several square miles. Their distribution is generally not continuous. Thus, although the distribution of Haplopappus divaricatus, $H$. validus subsp. torreyi, and $H$. rigidifolius appears to be sympatric in Bastrop and Lee counties, Texas (Fig. 2), they are allopatric for the most part. In Lee County, divaricatus and rigidifolius are sympatric at Tanglewood, but subsp. torreyi was found about 7, 17, and 23 miles south of Tanglewood, with the areas between apparently devoid of the three taxa. H. divaricatus was found again about 4 miles southeast of the extreme southern population of subsp. torreyi in the county.

A similar situation prevailed in Bastrop County, where divaricatus was found about 10 miles northeast of Bastrop, subsp. torreyi about 2 miles southeast and rigidifolius about 5 miles southeast of Bastrop. While sympatry of two or more of the taxa appears to be indicated in 10 counties in Texas (Fig. 2), it was actually observed in only a few cases, and in these cases the sympatry involved only $H$. rigidifolius and either $H$. divaricatus or $H$. validus subsp. torreyi.

Where two or more taxa were found to be sympatric, such as at Tanglewood, Texas (H. divaricatus \& H. rigidifolius) and at Palmetto State Park in Gonzales County, Texas ( $H$. rigidifolius \& $H$. validus subsp. torreyi), an attempt was made to locate hybrids between the taxa, but none
were found. However, there is an area in northern Texas, discussed later, in which it appears likely that subspecies validus and torreyi have hybridized.

Artificial hybridizations between the taxa were successful in 9 of the 10 possible combinations. Reciprocal crosses were lumped and considered the same when it became apparent that no significant differences in morphology or sterility could be detected between them. This was true of all crosses except those involving Haplopappus rigidifolius as the pistillate parent and in $H$. validus subsp. validus (pistillate) $\times$ subsp. torreyi (staminate) (see Fig. 3). Probably the failure of the $\mathrm{F}_{1}$ seedlings of the validus $\times$ torreyi cross and the few successful hybrids obtained in the reciprocal cross (torreyi $\times$ validus) was due to minor genetic differences accidentally introduced in the small size of the breeding stock used. Failure of crosses using $i$. rigidifolius as the pistillate parent, however, was consistent and presumably reflects a reciprocal difference, perhaps cytoplasmic in action. The relatively small number of hybridizations attempted (total of c. 40 heads crossed in each case) and the high sterility barrier, resulting in very few $\mathrm{F}_{1}$ 's in the crosses that succeeded, do not allow any definite conclusions to be made.

Assuming that pollen stainability can be taken as an index of fertility, there is no great sterility barrier among the subspecies of Haplopappus validus (Fig. 3). While subsp. graniticus and validus would appear to be able to exchange genes directly only with difficulty, there is an avenue for gene exchange through the intermediate subsp. torreyi, at least in the direction of validus to graniticus. These three taxa hence form a natural group.

The remaining two taxa, Haplopappus rigidifolius and $H$. divaricatus, are strongly isolated from the $H$. validus group, rigidifolius being more strongly isolated than divaricatus. Also, the isolation of these two taxa is phyletically in differing directions. The only hybridization of the 10 possible combinations among the taxa which failed was that between rigidifolius and divaricatus. It should be empha-
sized that $H$. rigidifolius $\times H$. divaricatus (and a few reciprocal) pollinations were performed many times in 1962, 1963, and 1964. The few achenes that did develop produced $2 n=10$ seedlings without exception. Whether these resulted from parthenogenesis or self-fertilization of $H$. rigidifolius is not known, but the latter is presumably the cause. "Selfing" is known in other self-incompatible Haplopappus taxa when stimulated by pollen from a related entity (Jackson, 1962).

Haplopappus rigidifolius is essentially totally isolated from all other members of the section, and is morphologically and cytologically the most distinct member of the section. It is not surprising that rigidifolius can occur sympatrically with $H$. divaricatus and $H$. validus subsp. torreyi with few or no hybridizations occurring.

In comparing the average pollen stainability of the $\mathrm{F}_{2}$ hybrid combinations (Table 3) with the $\mathrm{F}_{1}$ (Fig. 3), it can be seen that the average pollen stainability increases in the $F_{2}$. Indeed, a few $F_{2}$ plants in each category have regained nearly complete fertility. Most of these were, as far as chromosome number is concerned, reconstituted parental types. It is apparent that a minor amount of gene flow between all the taxa, including Haplopappus rigidifolius, is possible. But when one considers that (a) the taxa are mostly allopatric, (b) the reproductive effectiveness of the $\mathrm{F}_{1}$ hybrids is rather sharply reduced (based on the low pollen stainability of the $F_{1}$ and the low number of $F_{2}$ obtained), and (c) the average fertility of the $F_{2}$ is considerably below normal, it would appear that the amount of such gene flow is, at most, minor. It would seem quite likely that competition from normal individuals in the population would preclude the survival of most of the progeny resulting from the occasional hybridizations that might occur. The $H$. validus group may be exceptional in this respect.

In the field, hybrids would be much more likely to backcross with one of the parents than cross with each other to produce an $F_{2}$. However, the few backcross progeny obtained
indicate that average fertility in backcrosses would also be rather low.

There appear to be three natural groups among the taxa of section Isopappus: H. validus, $H$. divaricatus, and H. rigidifolius. Based on morphological differences, the geographical distributions, chromosome number differences, difficulty in obtaining $\mathrm{F}_{1}$ and $\mathrm{F}_{2}$ hybrids, and high sterility in the $\mathrm{F}_{1}$ and $F_{2}$, appropriate names are formally proposed for the taxa.

## SECTIONAL DESCRIPTION OF ISOPAPPUS

Mostly erect annual to weak perennial herbs, with alternate, spatulate, lanceolate, oblanceolate, to linear leaves, height to first head mostly about $25-65 \mathrm{~cm}$. Leaves setose-ciliate basally and glandular stipitate on the margins up to about $1 / 3-1 / 2$ their length, or, in one species (rigidifolius), not glandular stipitate but ciliate nearly over entire margin and more or less on the flat of the blade. Margins of median leaves irregularly serrate or serruate apically, or as much as the upper $1 / 3-3 / 5$ serrate, rarely entire (but commonly entire in rigidifolius). Stems striate, more or less glabrate basally. Peduncles with hispid or glandular stipitate, or both hispid and glandular stipitate pubescence; in one taxon (rigidifolius) sometimes with hirtellous, a low crisp-hairy pubescence, or even glabrous. Inflorescence a panicle, with heads of bright yellow or orangish-yellow flowers. Heads with fertile disc and ray flowers. Receptacle $1.8-7.0 \mathrm{~mm}$. wide. Involucres turbinate or, infrequently, hemispherical or cylindricturbinate. Phyllaries several-many, imbricated in several (c. 3) series, linear-attenuate to lanceolate, greenish, with scarious margins, strongly reflexed in age, with short glandular stipitate, hirtellous, glandular, or hispid and glandular stipitate pubescence on the back. Ray flowers $5-29$, pistillate, with conspicuous ligules (ligules $3.9-14.0 \mathrm{~mm}$ long, $1.7-5.0 \mathrm{~mm}$ wide). Disc flowers 6-108, perfect, the corolla gradually enlarged above the tube. Achenes subulate, about $2.0-3.2 \mathrm{~mm}$ long, serecious-canescent, stramineous to brown or redish-brown. Pappus a single series of equal (or nearly equal) capillary bristles, more or less ferruginous.

In the following key, and the descriptions which follow it, peduncle pubescence is based on the first 2.5 cm below the heads. Hispid pubescence at the base of bracts should be ignored. Floral measurements are based on fresh heads and on boiled heads from herbarium specimens.

KEY TO TAXA IN HAPLOPAPPUS, SECTION ISOPAPPUS
A. Peduncles hirtellous to hispid, with or without a lower, crisphairy pubescence intermixed, rarely glabrous, sometimes slightly
glutinous; plants leafy to summit, decumbent to erect; cauline leaves spatulate to lanceolate, entire (sometimes serrulate apically)

1. H. rigidifolius.
A. Peduncles obviously or densely glandular-stipitate pubescent, with or without hispid pubescence; plants not leafy to summit (leaves decreasing in size up the stem to small bracts above), erect; cauline leaves lanceolate to linear, serrate to serrulate apically (rarely entire)
B.
B. Number of ray flowers 6-9 (5-11) ; receptacle diameter about 3.0 mm (2.5-4.0)
2. H. divaricatus.
B. Number of ray flowers 13-21 (10-29) ; receptacle diameter 4.75.4 mm (3.5-7.0)
C. Peduncles with long-stiped, glandular-stipitate pubescence (longest hairs c. $0.4-0.5 \mathrm{~mm}$, including gland), often slightly hispid just below the heads; ligule width $2.0-2.8 \mathrm{~mm}$ (1.83.1) ; taxon of northern Texas and northward to central Kansas 3a. H. validus subsp. validus.
C. Peduncles with short-stiped, glandular-stipitate pubescence (longest hairs c. $0.2-0.3 \mathrm{~mm}$, including gland), never hispid; ligule width $2.6-4.2 \mathrm{~mm}$ (2.4-5.0); taxa of central and southern Texas D.
D. Ligule width $2.6-3.2 \mathrm{~mm}$ (2.4-3.3); occurs on sand and gravel of Coastal Plain from near Austin south to near the Gulf Coast (one exceptional population occurs near Carrizo Springs in Dimmit Co.) ...... 3b. H. validus subsp. torreyi.
D. Ligule width $3.2-4.2 \mathrm{~mm}$ (2.7-5.0) ; occurs exclusively in granite outcrop areas in and near the Central Mineral Region of Texas, rooted in cracks in the granite and in shallow sand deposits on the granite (one exceptional population occurs in coarse sand from c. 4-9 mi. se. of La Grange in Fayette Co.) .. 3c. H. validus subsp. graniticus.
3. Haplopappus rigidifolius Smith spec. nov.

Isopappus divaricatus (Nutt.) T.\&G. var. hirtellus Shinners, Field \& Lab. 18:157. 1950. (T: 10 mi . s. of Falfurrias, Brooks Co., Texas, C. L. \& A. A. Lundell 10813, smu!)
Croptilon divaricatum (Nutt.) Raf. var. hirtellum (Shinners) Shinners, Field \& Lab. 19:134. 1951.
Annual to weak perennial herb, decumbent to sprawling, or erect; stem highly variable in length, striate, strongly branched, with the basal branches often equalling or even exceeding the main axis in diameter; leaves rather rigid (hence: rigidifolius), alternate, spatulate to lanceolate, entire (occasionally serrulate apically), ciliate nearly over entire margin and often on the flat surface of the blade, about $2.5-4.5(2.0-5.8) \mathrm{cm}$ long and $0.2-0.5(0.2-0.8) \mathrm{cm}$ wide; peduncles hirtellous to hispid, often with a lower crisp-hairy pubescence inter-
mixed, sometimes slightly glutinous, rarely glabrous; heads several in a somewhat closed or compact panicle; receptacle diameter 2.9-4.0 (1.8-5.0) mm ; phyllaries narrowly lanceolate, acuminate, c. $4.5-7.0 \mathrm{~mm}$ long and $1.0-1.6 \mathrm{~mm}$ wide; rays $9-21$ ( $5-22$ ) ; ligules $4.5-6.3$ (4.0-7.4) mm long and 2.0-2.5 (1.7-2.6) mm wide; disc corollas 25-45 (6-60); achenes subulate, serecious-canescent, $2.0-2.4 \mathrm{~mm}$ long, stramineous to pale reddish-brown, sometimes mottled. Chromosome number $n=5$.

Blooms September-November and later. Distinguished easily from other taxa in the section by its lack of glandular stipitate pubescence on the peduncles. Known from 23 counties in southern Texas (Fig. 2).

A new epithet is required for this species under Haplopappus, since the name $H$. hirtellus had previously been used for a species from Chile (Hall, 1928).

Haplopappus rigidifolius is highly variable, especially with regard to number of disc and ray flowers, as well as general size. Collections range from strictly decumbent, weak perennials with stems less than 10 cm long and small heads (Aransas and Victoria counties, Texas) to erect annuals with stems as much as 70 cm or more long and large heads (Live Oak and Refugio counties, Texas). There is some correlation of the above characteristics with distance from the ocean, but the variation is not strictly clinal. The coastal, decumbent population might be considered a seacoast ecotype, as in Succisa pratensis, Matricaria inodora (Stebbins, 1950), Clarkia prostrata, or C. davyi (Lewis \& Lewis, 1955). Taxonomic recognition of the variation does not, however, appear justifiable, since there is considerable intergradation and, even in the same population, some heterogeneity for the characters mentioned.
Representative Specimens: TEXAS: Aransas Co., Goose Island State Park, Smith 91, kanu, Johnston 53.280.174, tex ; Austin Co., 4.8 mi . s. of Kenney, Smith 259, Kanu; Bastrop Co., 5.1 mi . se. of Bastrop, Smith 553, Kanu; Bee Co., c. 21.2 mi . w. of junction of 202 \& US 183, Smith 635, Kanu, Smu, Ga, Fsu, \& nCu; Burleson Co., 1.1 mi . s. of Somerville, Smith 260, kanu; Colorado Co., 3 mi . s. of junction of $71 \&$ US 90A, Smith 257, Kanu; Gonzales Co., near Palmetto State Park, Smith 243, kanu; Karnes Co., 2.5 mi . ne. of Kenedy, Johnson 1354, Smu, tex; Kenedy Co., 0.5 mi . n. of Sarita, Smith 92, kanu, 5 mi. n. of Armstrong, Turner 4474, tex; Kleberg Co., King Ranch, Johnston 54416, tex; Lavaca Co., $13 \mathrm{mi} . \mathrm{n}$. of Hallettsville, Shinners

28701, smu; Lee Co., at Tanglewood, Smith 236, kanu; Medina Co., near Devine, Barkley 13947, fsu, tex; Nueces Co., 1 mi . s. of Flour Bluff, Jones 745, smu; Refugio Co., c. 4 mi . w. of junction of 202 \& US 183, Smith 638, kanu \& tex; Victoria Co., 2.0 mi . sw. of Inez, Smith 252, Kanu, 8.3 mi . sw. of Victoria, Shinners 25235, SMU; Wharton Co., 3.7 mi . s. of Nada, Smith 256, kanu; Willacy Co., 4 mi . w. of Redfish Bay, Johnston 54179, tex. Also known to occur on Padre Island.
2. Haplopappus (Isopappus) divaricatus (Nutt.) Gray, Explor. Railroad Route Miss. River to Pacific 4:99. 1856. (as "Aplopappus").
Inula divaricata Nuttall, Gen. 2:152. 1818. (T: vicinity of Savannah in Georgia, perhaps PH)
Chrysopsis divaricata (Nutt.) Elliot, Bot. Sketch 2:338. 1824.
Croptilon divaricatum (Nutt.) Raf., Fl. Tellur. 2:47. 1836.
Diplopappus divaricatus (Nutt.) Hook., Comp. Bot. Mag. 1:97. 1836.

Isopappus divaricatus (Nutt.) T.\& G., Fl. N. A. 2:239. 1842. Aster divaricatus (Nutt.) Kuntze, Rev. Gen. 1:318. 1891.
Annual herb, erect, virgate before fully in bloom; stem 4.0-7.0 (2.0-11.5) dm high, striate, glabrate basally, glandular stipitate at the apex, more or less ferruginous; leaves alternate, basal ones oblanceolate to spatulate, entire to irregularly serrate, setose-ciliate at the base, 9-12 ( $7-14$ ) cm long, $1.5-2.0 \mathrm{~cm}$ wide; median leaves lanceolate, irregularly serrate, occasionally one or more doubly serrate, setoseciliate at the base, glandular stipitate on the margins, 3-5 (2.8-8.0) cm long, $0.2-0.4(0.15-1.5) \mathrm{cm}$ wide; peduncles with mixed glandular stipitate and hispid pubescence, infrequently to rarely not hispid; heads many in an open panicle; receptacle diameter 2.8-3.4 (2.5-4.0) mm ; phyllaries lanceolate, the largest c. $1 \times 5 \mathrm{~mm}$, short glandular stipitate and sparsely hispid on the back; rays $6-9$ ( $5-11$ ) ; ligules 4.5-6.0 (3.9-6.0) mm long and 2.0-2.6 (1.9-3.2) mm wide; disc corollas 14-22 (9-26); achenes c. 2 mm long, subulate, somewhat sparsely serecious-canescent, stramineous to reddish-brown. Chromosome number $n=4$.

Blooms late August-October. Distinguished from $H$. rigidifolius by its glandular-stipitate pubescence on the peduncles, and from other members of the section by its small heads and low number of ray and disc flowers. Known from 266 counties in 11 states (Fig. 2).

A casual weed in most areas of occurrence, Haplopappus divaricatus becomes very abundant in sandy areas in Georgia and South Carolina. The distribution of H. divaricatus
is apparently divided into an eastern and a western population by the broad band of river alluvium in the southern Mississippi River valley (see Baker, 1936; Plate 4). H. divaricatus, as well as other taxa in the section, appear to be poor competitors on soils high in clay or low in sand.

The infrequent to rare form with peduncles glandularstipitate pubescent only (no hispid pubescence) appears to be localized in a few areas at the western and southwestern edge of the distribution and does not appear to be worthy of taxonomic recognition. Haplopappus divaricatus specimens lacking hispid pubescence on the peduncles are sometimes similar to depauperate specimens of $H$. validus subsp. torreyi.

Representative Specimens: ALABAMA: Butler Co., 6.1 mi. ne. of junction of US $31 \&$ Ala. 10, Smith 538, Kanu; Chambers Co., 0.1 mi . sw. of junction of road $147 \&$ US 431, Smith 479, kanu; Henry Co., 8.3 mi . s. of Abbeville, Smith 537, Kanu; Lee Co., 10.8 mi . w. of junction of $40 \& 29$ in Auburn, Smith 478, kanu; Washington Co., c. 0.5 mi. s. of Choctaw Co. line on US 17, Smith 539, Kanu. ARKANSAS: Cleveland Co., 1.6 mi . w. of Kingsland, Smith 457, kanu; Dallas Co., just e. of Manning, Smith 456, kanu; Little River Co., 2 mi . n. \& $2.6 \mathrm{mi} . \mathrm{w}$. of Winthrop, Smith 128, kanu. FLORIDA: Alachua Co., just sw. of Archer, Smith 529, Kanu; Gilchrist Co., just outside of Wilcox, Smith 527, Kanu; Jackson Co., at Marianna Caverns State Park, Mitchell 897, FSU; Lake Co., 16.3 mi . ssw. of Leesburg, Smith 533, Kanu; Leon Co., vicinity of Silver Lake, Godfrey 60356, FSU. GEORGIA: Bartow Co., 2.1 mi. s. $52^{\circ}$ w. of Allatoona Dam, Duncan 8887, ga; Clarke Co., vacant lot in Athens, Cronquist 4132, GA; Dougherty Co., R.R. yards in Albany, Thorne 5856, Ga; Emanuel Co., 9 mi. e. of Adrian, Wilbur 2923, ga; Greene Co., 3.7 mi . se. of Siloam, Smith 492, kanu. LOUISIANA: Bienville Co., 2.2 mi. e. of Hagewood, Smith 54s, kanu; DeSoto Co., 3.6 mi . nw. of Keatchie, Smith 274, Kanu; Nachitoches Co., 2.1 mi. e. of Hagewood, Smith 544, kanu, smu, \& tex; Ouachita Co., 1 mi . e. of Calhoun exit on Interstate 20, Smith 542, kanu; Sabine Co., 3.9 mi . s. of Zwolle, Smith 273, KANU. MISSISSIPPI: JASPER Co., 2.7 mi w. of junction of $504 \& 503$, Smith 462, kanu; Lauderdale Co., near Meridian, Smith 464, kanu; Newton Co., dry ridge thickets, Demaree 36155 , FSU, 4.3 mi . nw. of junction of Miss. 504 \& 503, Smith 460 , kanu. NORTH CAROLINA: Anson Co., 2.6 mi . se. of Morvin, Smith 510, kanu; Bladen Co., s. of Elizabethtown, Smith 513, kanu; Harnett Co., c. 4 mi . w. of Mamers, Laing 251, ga; Lee Co., 7.5 mi . e. of Sanford, Smith 512, kanu; Montgomery Co., 1.3 mi . n. of Can-
dor, Smith 511, kanu. OKLAHOMA: McCurtain Co., 0.5 mi. n. of Tom, Waterfall 10496, tex; Pushmataha Co., 7 mi . w. of Antlers, Waterfall 11147, tex. SOUTH CAROLINA: Aiken Co., 1.1 mi n. of Aiken, Smith 501, kanu ; Charleston Co., 1.9 mi . e. of junction of S.C. 174 \& US 17, Smith 521, kand; Fairfield Co., c. 5 mi . w. of Rockton, Smith 507, kanu; Greenwood Co., 0.2 mi. e. of Abbeville Co. line on S.C. 72, Smith 499, kanu; Kershaw Co., 6.2 mi. w. of junction of S.C. 34 \& US 1, Smith 508, Kanu; Lexington Co., 1.1 mi. n. of Aiken Co. line on S.C. 215, Smith 502, kanu. TEXAS: Anderson Co., $6 \mathrm{mi} . \mathrm{nw}$. of Tennessee Colony, Marsh 283, tex; Bastrop Co., 8.2 mi . sw. of junction of $21 \&$ US 290, Smith 554, Kanu; Fannin Co., 1.4 mi. e. of Telephone, Smith 286, kanu; Freestone Co., 12 mi. ese. of Fairfield, Turner 4438, tex; Lee Co., at Tanglewood, Smith 237, kanu; Leon Co., 5 mi. e. of Buffalo, Gould 7276, tex; Limestone Co., 5.5 . mi. e. of Kosse, Shinners 30574, smu; Milam Co., 6.1 mi . se. of junction of $36 \&$ US 79, Smith 558, Kanu; Morris Co., 2 mi. se. of Daingerfield, Whitehouse 17656, SMU; Nacogdoches Co., Cushing, Tharp \& Brown 53-8, TEX; Rains Co., 5 mi. s. of Emory, Smith 562, kanu; Robertson Co., 0.5 mi . sw. of Hearne, Smith 560, kanu, near New Baden, Tharp \& Barkley 13978, tex; Titus Co., 1.6 mi. ese. of Mt. Pleasant, Shinners 16079, smu; Trinity Co., 1.9 mi . nw. of Groveton, Smith 266, kanu; Upshur Co., 1.5 mi. e. of Big Sandy, King 2179, tex; Van Zandt Co., 5.7 mi . se. of Willis Point, Shinners 8469, Smu.

3a. Haplopappus validus (Rydb.) Cory Rhodora $38: 406$. 1936. (as "Aplopappus") subsp. validus
Isopappus validus Rydberg, Brittonia 1:100-101. 1931. (T: 6 mi . s. of Ellinwood, Barton Co., Kansas, P. A. Rydberg \& R. Imler 1309, Ny. Paratypes: Rudberg \& Imler 616 \& 721 KANU).

Anrual (facultative winter annual) herb, erect; stem 4.5-6.5 (3.0$7.5) \mathrm{dm}$ high, striate, glabrate basally, glandular stipitate above; leaves alternate, basal ones oblanceolate to spatulate, entire to irregularly serrate, setose-ciliate at the base, 7-9 (6-10) cm long, 1.9-2.3 (1.2$3.0) \mathrm{cm}$ wide; median leaves lanceolate, irregularly serrate, setoseciliate at the base, glandular stipitate on the margins, 4.5-6.5 (3.0-8.0) cm long, mostly $0.3-1.2 \mathrm{~cm}$ wide; peduncles with glandular stipitate pubescence, the stipes rather long ( $0.4-0.5 \mathrm{~mm}$, including gland), often sparsely hispid, especially just below heads; heads several in a somewhat rigid panicle; receptacle diameter 4.7-6.0 (4.0-7.0) mm; phyllaries lanceolate, the largest about $1.1 \times 6.8 \mathrm{~mm}$, short glandular stipitate, and sometimes sparsely hispid, on the back; rays $16-23$ (13-29) ; ligules $7-10$ ( $6-12$ ) mm long and 2.0-2.8 (1.8-3.1) mm wide; dise corollas $55-70$ (33-108); achenes 2.2-2.6 (2.0-3.0) mm long; subulate, serecious-canescent, stramineous to reddish-brown. Chromosome number $n=5$.

Blooms July-early October. Distinguished from Haplopappus validus subsp. torreyi and subsp. graniticus by its narrower ligules, from $H$. rigidifolius by its glandularstipitate pubescence on the peduncles, and from $H$. divaricatus by its larger heads. Known from 60 counties in Kansas, Oklahoma, and nothern Texas (Fig. 2).

This subspecies is mostly limited to relatively small populations in sandy areas along rivers and fence rows, except in the stationary sand dunes in the Big Bend area of Kansas where it assumes great abundance.

Marked seedlings have been observed to withstand prolonged subfreezing temperatures and grow to maturity the following summer. Seedlings of the outer taxa in the section are rapidly killed by the first severe frost.

Populations of subsp. validus in nothern Texas, east of the Panhandle, are almost uniformly atypical for the taxon. This is especially true of Parker, Johnson, Tarrant, Dallas, Wise, Denton, McLennan, and Callahan counties. They nearly all lack hispid pubescence on the peduncles and have smaller heads with fewer flowers than usual. It is believed that most populations in these counties are carrying one or more subsp. torreyi chromosomes, or at the very least, have picked up subsp. torreyi genes through hybridization. Numerous somatic chromosome counts from these populations were nearly all $2 n=10$. However, one $2 n=11$ and a few $2 n=12$ counts were made. One count of $2 n=10$ showed a heteromorphic pair, one homologue of which could have been from subsp. torreyi. It is hoped that further study, including genetic analyses, will confirm the hybrid nature of certain individuals in these populations.

Representative Specimens: KANSAS: Dickinson Co., 2.9 mi . w. of Abilene, Smith 122, Smu; Ellsworth Co., 0.5 mi. e. of 'Ierra Cotta, Smith 121, KANU; Kiowa Co., 3 mi . w. of Greensburgh, McGregor 4041, kanu; McPherson Co., McPherson County State Park, Smith 120, tex; Reno Co., 10 mi . w. of Hutchinson, Wagenknecht 3124, kanu; Rice Co., 8.8 mi . e. of Sterling, Smith 118, kanu. OKLAHOMA: CADDO Co., 5.9 mi . e. of junction of US $281 \&$ Okl. 9 , Smith 605 , kanu; Canadian Co., $1.4 \mathrm{mi} . \mathrm{n}$. of El Reno, Smith 220, kanu; Grant Co., $1.7 \mathrm{mi} . \mathrm{n}$. of junction of US $60 \&$ US 81, Smith 218, Kanu; Jefferson Co., 0.2 mi . n. of Red River off US 81, Smith 227, kanu;

Major Co., 1 mi e. \& $1 \mathrm{mi} . \mathrm{s}$. of Cleo Springs, Richards 1093, kanu, 1 mi . ne. of Orienta, Waterfall 10354, tex. TEXAS: Callahan Co., 15 mi . se. of Abilene, Henderson 62-1182, fsu (rather atypical), Henderson 63-1772, tex; Grayson Co., 4 mi. ese. of Gainsville, Smith 564, kanu; Hemphill Co., 7 mi . ne. of Canadian, Rowell 4259, tex; Hood Co., 5.5 mi . ne. of Granbury, Shinners 10330, Smu; Lipscomb Co., 3.5 mi. sw. of Higgens, Cory 50288, smu; McLennan Co., n. of Gholson, Smith 928, tex; Montague Co., 7.6 mi . e. of junction of US 82 \& US 81, Smith 565, kanu ; Somervell Co., 2.8 mi . ne. of Glen Rose, Shinners 13812 , SMU.
3b. Haplopappus validus (Rydb.) Cory subsp. torreyi Smith, subspec. nov.
Isopappus hookerianus T. \& G., Fl. N. A. 2:239. 1842. (T: near Gonzales, Gonzales Co., Texas, Drummond 184, K, photograph!) not Haplopappus hookerianus DC., 1838.
Aster hookerianus (T. \& G.) Kuntze, Revis. Gen. 1:318. 1891.
Croptilon hookerianum (T. \& G.) House, N.Y. State Mus. Bul. 223-234:61. 1921.
Isopappus divaricatus (Nutt.) T. \& G. var. hookerianus (T. \& G.) Shinners, Field \& Lab. 18:157. 1950.
Croptilon divaricatum (Nutt.) Raf. var. hookerianum (T. \& G.) Shinners, Field \& Lab. 19:134. 1951.
Haplopappus divaricatus (Nutt.) Gray var. hookerianus (T. \& G.) Waterfall, Rhodora 62:321. 1960.
Annual herb, erect; stem c. 3-6 dm high, striate, glabrate basally, glandular stipitate above; leaves alternate, basal ones oblanceolate to spatulate, entire to irregularly serrate, setose-ciliate at the base, $8-10(6-12) \mathrm{cm}$ long and $1.5-2.0(1.2-2.5) \mathrm{cm}$ wide; median leaves lanceolate to linear, irregularly serrate, setose-ciliate at the base, glandular stipitate on the margins, 4-8 (3.2-10.0) cm long and $0.3-0.8$ (0.2-1.1) cm wide; peduncles not hispid, densely glandular stipitate, the stipes short (longest c. $0.2-0.3 \mathrm{~mm}$, including gland); heads several in a spreading panicle, the peduncles sometimes reclinate; receptacle diameter $4.5-5.1(3.5-6.0) \mathrm{mm}$; phyllaries lanceolate, the largest c. $1 \times 6 \mathrm{~mm}$, short glandular stipitate on the back, not hispid; rays 12-16 (10-17); ligules 7.0-9.2 (5.7-11.0) mm long and 2.6-3.2 (2.4-3.3) mm wide; disc corollas 33-47 (23-51); achenes c. 2.2 mm long, subulate, densely serecious-canescent, stramineous to pale brown. Chromosome number $n=6$.

Blooms August-October. Distinguished from Haplopappus rigidifolius by its glandular-stipitate pubescence on the peduncles; from $H$. divaricatus and $H$. validus subsp. validus by its lack of hispid pubescence on the peduncles or phyllaries and its wider ligules; and from $H$. validus subsp.
graniticus by its narrower ligules and its ecology (never occurs in granite outcrop areas). Known from 15 counties in southern Texas (Fig. 2).

This subspecies is noteworthy for the paucity of individuals in most observed populations. Except for two populations in Refugio Co., Texas, it has not been observed to approach the abundance of other taxa in the section.
Representative Specimens: TEXAS: Aransas Co., Rockport, Tharp 42-81, tex; Bastrop Co., 1.5 mi . se. of Bastrop, Smith 79, ga; Caldwell Co., 4.8 mi . se. of Prairie Lea, Smith 244, Kanu; Goliad Co., 9.5 mi . s. of Goliad, Shinners 25210, smu; Gonzales Co., near Palmetto State Park road 11 exit, Smith 242, kanu, Gonzales, Tharp (no number), tex; Karnes Co., 1.5 mi. e. of Harmony School near Ecleto Creek Crossing, Johnson 996, smu, tex ; Lee Co., 2.3 mi . n. of Giddings, Smith 240, kanu, 0.8 mi . w. of Manheim, Smith 557, tex; Refugio Co., 3.4 mi . w. of junction of 202 \& US 183, Smith 639 , KANU \& NCU, 3 mi . e. of Woodsboro, Jones 725, smu; Victoria Co., 2.8 mi . se. of Raisin Smith 251, smu.

3c. Haplopappus validus (Rydb.) Cory subsp. graniticus Smith subspec. nov. (T: 1.9 mi . e. of Streeter, Mason Co., Texas, E. B. Smith 624 , KANU. Isotype: SMU \& NCU)
Herba annua, 3-6 dm alta; caulibus unicis, erectis, striatis, subtus in maturitate tomentosis vel glabratis et saepe ramosis, insuper stipitoglandulosis; foliis alternis, linearibus vel lanceolatis, serratis, subtus ciliatis, ad 8 cm longis et 1 cm latis, margininibus stipito-glandulosis; capitulis pluribus, paniculatis; disco dia. 4.5-5.5 (3.9-6.0) mm ; phyllariis anguste lanceolatis, acuminatus, ca. 7.5 mm longis et 1.5 mm latis, dorsis sparse stipito-glandulosis; radiis (10-) 13-21; ligulis 8-12 (6.3-14.0) mm longis et $3.2-4.2(2.7-5.0) \mathrm{mm}$ latis; disci corollis 35-65 (20-79), $5.0-6.5 \mathrm{~mm}$ longis; achaeniis subulatis, pubescentis, 2.3-3.2 mm longis; pappis $2.5-4.0 \mathrm{~mm}$ longis.

Annual herb, $3-6 \mathrm{dm}$ tall; stem solitary, erect, striate, tomentose to glabrate below in maturity and often basally branched, glandular stipitate above (peduncles); leaves alternate, linear to lanceolate, serrate, ciliate basally, up to 8 cm long and 1 cm wide, glandular stipitate on the margins; heads several in an open panicle; disc dia. 4.5-5.5 (3.9-6.0) mm ; phyllaries narrowly lanceolate, acuminate, c. 7.5 mm long and 1.5 mm wide, sparsely glandular stipitate on the back; rays (10-) 13-21; ligules $8-12$ (6.3-14.0) mm long and mostly 3.2-4.2 (2.7-5.0) mm wide; disc corollas $35-65$ (20-79), $5.0-6.5 \mathrm{~mm}$ long; achenes subulate, pubescent (serecious-canescent), $2.3-3.2 \mathrm{~mm}$ long; pappus a single row of equal bristles, $2.5-4.0 \mathrm{~mm}$ long. Chromosome number $n=7$.

Blooms August-October. Distinguished from Haplopap-
pus rigidifolius by having glandular-stipitate pubescence on the peduncles; from $H$. divaricatus and $H$. validus subsp. validus by its lack of hispid pubescence on the peduncles or phyllaries and its wider ligules; and from H. validus subsp. torreyi by its wider ligules and ecology (occurs almost exclusively in granite outcrop areas). Known from 5 counties in central Texas (Fig. 2).

The flowers of subsp. graniticus are a deeper yellow than those of other members of the section. However, the difference is not very noticeable until specimens are compared side by side.

Except for the Fayette Co. population mentioned in the key, subsp. graniticus is limited exclusively to granite outcrop areas in and near the Central Mineral Region of Texas (see Tharp, 1952) or granitic Central Basin (see Gould, 1962). The Fayette Co. population grows in coarse sand and resembles subsp. torreyi. Subspecies torreyi and graniticus overlap in morphology, but the overlap is greater in this population. While some members of the population key easily to subsp. graniticus, others key to subsp. torreyi. Cytological examination of numerous individuals from the population showed them all to be $2 n=14$ or $n=7$. Therefore, the whole population is presumed to be subsp. graniticus. The fact that this population could not be placed, with certainty, in either subsp. graniticus or torreyi without cytological examination is one of the main reasons for placement of graniticus and torreyi at the subspecific level.
Representative Specimens: TEXAS: Burnet Co., Inks Lake State Park, 1.8 mi. s. of Park Headquarters, Smith 76, kanu; Fayette Co., 8.6 mi. se. of La Grange, Smith 649 , KANU (somewhat atypical); Llano Co., Enchanted Rock, Whitehouse 10303, smu; Mason Co., 2 mi . s. of Air (also called Camp Air), Smith 622, kanu, GA, tex, \& FSU, and $31 / 4 \mathrm{mi}$. w. of Fredonia, Cory 43052, smu, Cory 43051, tex. DEPARTMENT OF BOTANY, RUTGERS THE STATE UNIVERSITY, NEWARK, NEW JERSEY

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